

EDIACARAN FOSSILS FROM THE SEKWI BROOK AREA, MACKENZIE MOUNTAINS, NORTHWESTERN CANADA

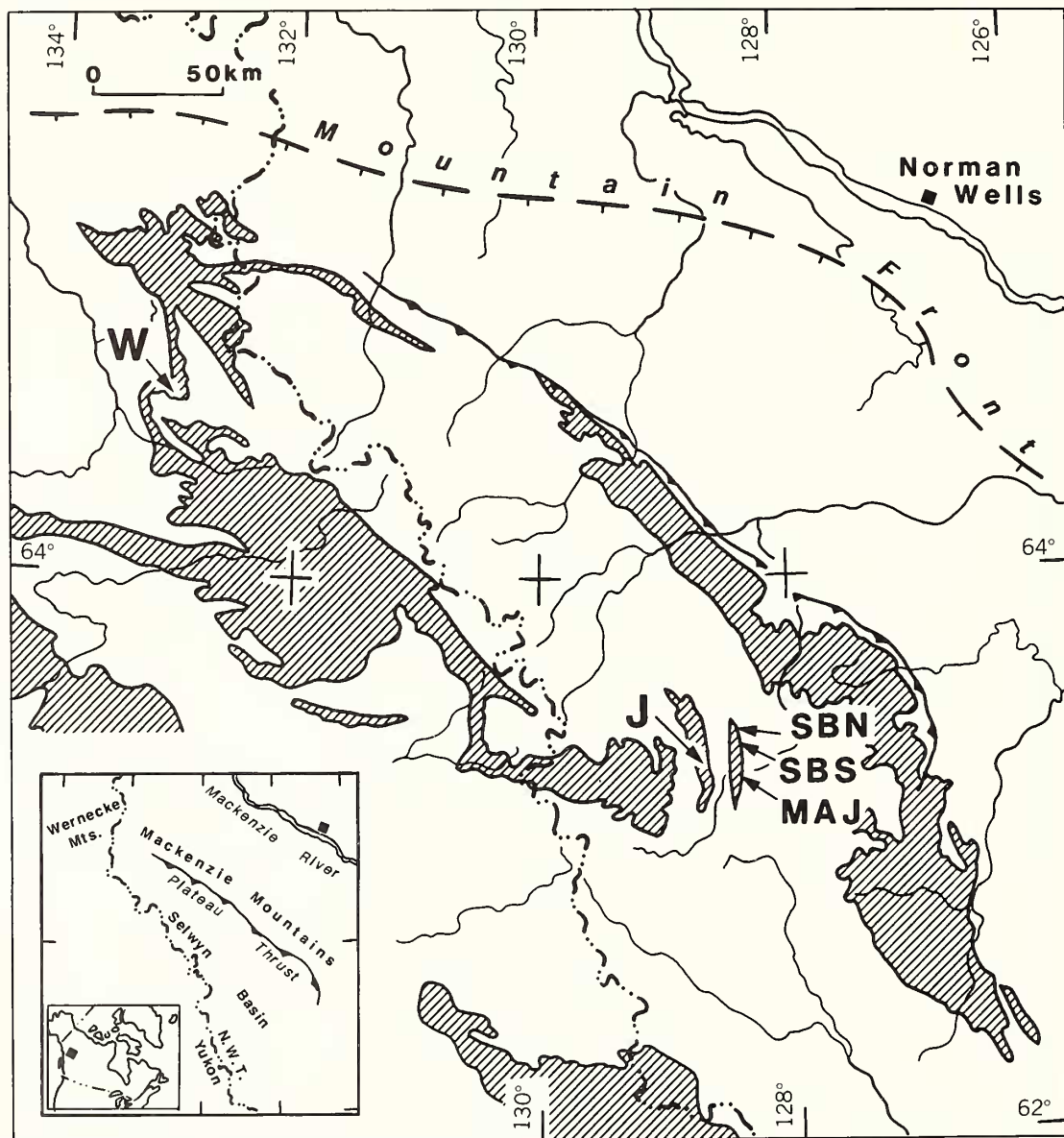
by GUY M. NARBONNE and JAMES D. AITKEN

ABSTRACT. Ediacaran body fossils and trace fossils occur sporadically throughout more than one kilometre of strata in the upper part of the Windermere Supergroup in the western Northwest Territories of Canada. The oldest fossiliferous unit, the Sheepbed Formation, contains body fossils (*Beltanella gilesi*, *Charniodiscus?* sp., *Cyclomedusa plana*, *Cyclomedusa* sp., *Eoporpita* sp., *Kullingia* sp. and *Medusinites asteroides*) and very rare trace fossils (*Planolites montanus*). The Blueflower Formation contains rare body fossils (*Charniodiscus?* sp., *Ediacaria* sp., *Inkrylovia* sp., *Pteridinium* sp. and *Sekwia excentrica*) and abundant trace fossils (*Aulichnites* ichnosp., *Helminthoidea* ichnosp., *Helminthoidichnites tenuis*, *Helminthopsis abehi*, *Helminthopsis irregularis*, *Helminthopsis?* ichnosp., *Lockeia* ichnosp., *Neonereites* ichnosp., *Palaeophycus tubularis*, *Planolites montanus*, *Torrowangea rosei* and a knotted burrow). Overlying dolostones and thick-bedded sandstones of the Risky Formation contain only simple trace fossils (*Palaeophycus tubularis*, *Planolites montanus*). The Sekwi Brook biota lived in a deep-water, basin slope setting below storm wave-base. Most of the body fossils probably represent benthic polypoid and frond-like organisms. The body fossil assemblage is broadly similar to that described from correlative shallow shelf deposits in the Wernecke Mountains, Flinders Ranges and Russian Platform. The trace fossil assemblage is dominated by simple and irregularly meandering burrows, but contains some patterned meanders typical of the *Nereites* ichnofacies. The occurrence of this relatively diverse, mainly deep-water assemblage of benthic body fossils and infaunal burrows indicates that the initial radiation of metazoans extended to the deep sea, and that some aspects of Phanerozoic-style marine ecosystems were initiated during the earliest stages of metazoan evolution.

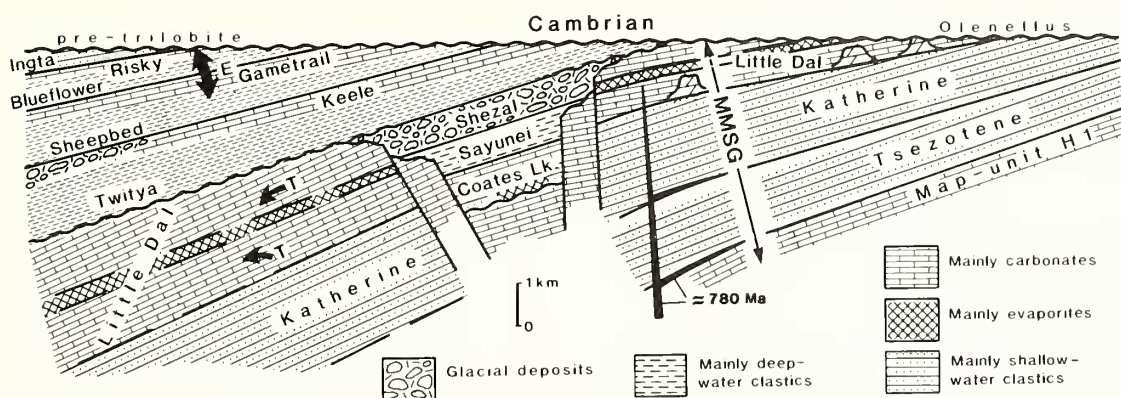
THE Ediacaran fauna represents the oldest diverse assemblage of megascopic animals and trace fossils in the world, and consequently the rootstock from which all subsequent metazoans evolved. Ediacaran animal remains are predominantly discoid and pennate fossils (commonly interpreted as primitive cnidarians) with fewer arthropods, echinoderms and problematic taxa. Trace fossils are chiefly simple subhorizontal burrows with rarer meandering forms. Recent summaries of this fauna can be found in Glaessner (1984) and Sokolov and Ivanovskiy (1985).

The Ediacaran assemblage is of latest Precambrian age, and consistently occurs between the highest Proterozoic tillites and the lowest Cambrian-type shelly fossils and trace fossils (Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984). It was first reported from Namibia and South Australia, but subsequently has been documented from more than twenty-five localities around the world (Glaessner 1984, fig. 1/8; Hofmann 1987, fig. 13). The first description of Ediacaran fossils from Laurentia (= ancestral North America) was by Hofmann (1981), who collected body fossils and trace fossils from the Sekwi Brook area of the Mackenzie Mountains (Text-fig. 1) during a brief visit of the I.U.G.S. Precambrian–Cambrian Boundary Working Group (Fritz 1980). Hofmann reported the body fossils *Inkrylovia* sp. and *Sekwia excentrica*, the trace fossils *Torrowangea* sp. and *Gordia* sp. and several problematica and dubiofossils. Aitken (1989a) subsequently figured a specimen of the megafossil *Pteridinium* sp. from the same locality, Baudet *et al.* (1989) studied the acritarchs from this section, and Aitken and Narbonne (1989) described cryptalgal structures from a nearby section. Ediacaran body fossils and ichnofossils have also been described from age-equivalent shallow shelf deposits in the Wernecke Mountains (Text-fig. 1), 250 km west north-west of Sekwi Brook (Hofmann *et al.* 1983; Narbonne and Hofmann 1987).

During June 1988, the present authors collected Ediacaran fossils from Hofmann's (1981) locality and two others in the Sekwi Brook area of the Mackenzie Mountains (Text-fig. 1) as part of a regional study of the upper Precambrian strata. These collections considerably extend the known diversity and stratigraphic range of Ediacaran fossils in the Mackenzie Mountains. Previous reports of Ediacaran fossils have been mainly from shallow shelf settings (e.g. Flinders Ranges, Russian Platform, Wernecke Mountains) with fewer reports from deep slope/fan environments (e.g. Newfoundland, Charnwood Forest). The occurrence of a relatively diverse assemblage of body



TEXT-FIG. 1. Location of study sections in the Mackenzie Mountains. Outcrop of the Windermere Supergroup is shaded. SBN = Sekwi Brook North; SBS = Sekwi Brook South; MAJ = Majesty Property. Other fossiliferous Ediacaran sections described previously are in the June Lake Anticline (J) and in the Wernecke Mountains (W).



TEXT-FIG. 2. Regional stratigraphic setting of the Ediacaran biota from Sekwi Brook. E = Ediacaran fossils; T = *Chuarina-Tawuia* assemblage; MMSG = Mackenzie Mountains Supergroup.

fossils and trace fossils in basin slope deposits at Sekwi Brook permits more detailed evaluations of the palaeoenvironmental affinities of Ediacaran organisms. In this paper, description of the fossils and discussion of their significance are by Narbonne; information on the stratigraphy and depositional environments of the strata is by Aitken.

STRATIGRAPHIC AND PALAEOENVIRONMENTAL SETTING

The terminal Proterozoic formations of the Mackenzie and Wernecke Mountains (Text-figs 1 and 2) are assigned to the upper part of the Windermere Supergroup. The base of the Windermere is marked by the onset of rifting at 770–780 Ma (Armstrong *et al.* 1982; Eisbacher 1981, 1985; Jefferson and Ruelle 1986). The top is the base of Cambrian strata.

The terminal Windermere Formations make up four, kilometre-scale, shallowing-upward, carbonate-capped Grand Cycles (*sensu* Aitken 1966, 1978), as follows (Aitken 1989a):

4. Ingta Formation (230 m)
3. Blueflower (550 m) and Risky (150 m) Formations
2. Sheepbed (900 m) and Gametrail (300 m) Formations
1. Twitya (900 m) and Keele (500 m) Formations

These cyclical deposits post-date, and pass without noticeable effect, across the sites of the rift-depressions in which the older Windermere deposits, the Coates Lake and Rapitan groups, were deposited (Text-fig. 2). Evidence for a Rapitan glaciation is well known (Young 1976; Yeo 1981; Eisbacher 1981, 1985). The deposits of a second Late Proterozoic glaciation, which directly underlie the Sheepbed Formation, have thus far been described only in oral presentations with published abstracts (e.g. Aitken 1987, 1989b).

The middle two of the upper Windermere Grand Cycles (Sheepbed-Gametrail, Blueflower-Risky) contain abundant Ediacaran megafossils (this study). The uppermost Windermere Grand Cycle, the Ingta Formation, yields abundant, well-preserved trace fossils, but lacks both diagnostically Cambrian traces and body impressions of Ediacaran type. We interpret it as latest Precambrian. The Ingta, and in other places all of the other terminal Proterozoic formations, are unconformably overlain by correlatives of the Backbone Ranges and Vampire Formations bearing Early Cambrian trace fossils and small shelly fossils (Fritz *et al.* 1983; Narbonne *et al.* 1985; Nowlan *et al.* 1985). The position, in basinward areas such as Sekwi Brook, of the major unconformity beneath the typical Backbone Ranges Formation is in dispute (reviewed by Aitken 1989a).

Sheepbed Formation

The Sheepbed Formation of the Sekwi Brook area is much coarser, on average, than in the 'typical' belt of exposures above the Plateau Thrust. The lower part, below the lowest fossils found, contains rare packets of thick and very thick beds of quartzose sandstone that are normally graded and in part coarse-grained (Bouma

Ta). Rare packets of ribbon-bedded lime mudstone are also present. Because of their association with and involvement in mass-transport deposits, and normal grading seen in minor beds with a content of coarser allochems, they are interpreted as turbidites. The upper (fossiliferous) part is dominated by laminated to finely laminated, dolomitic interstone and very fine-grained sandstone, with partings and packets of dark grey to brown, silty shale and mudstone. Sole marks are present, but rare. The thin sandstones are Bouma Tb, Tbc, and Tc units. The content of dolomitized and undolomitized, ribbon-bedded lime mudstone (turbidites), monomict, matrix-supported carbonate breccias (debris flows), and penecontemporaneous folds and slide masses is highly variable along strike. The thickness in the Sekwi Brook area is not determinable, but is almost certainly greater than the maximum of 800 m in the 'typical' outcrop belt.

Interpretation of the depositional environment begins with the observation that the 'typical' Sheepbed to the north-east contains very little sand-grade or coarser siliciclastic material. The Gametrail Formation (carbonates, there partly in a shallow-water facies) that intertongues with and overlies the upper Sheepbed, also lacks siliciclastic detritus. The 'typical' Sheepbed overlies the deeply drowned Keele platform, whereas Sekwi Brook lies outboard of the Keele platform margin, above a previously-existing bathymetric basin or trough. It is precisely at Sekwi Brook that coarse-grained, thick-bedded, turbiditic sandstones occur in the lower Sheepbed. These sandstones appear to be deep-sea fan-channel deposits (Mutti and Normark 1987; Shanmugam and Moiola 1988), transported axially along the inherited off-platform trough. The upper part of the formation is readily interpreted as a complex of slope deposits that accumulated below storm wave-base. This is consistent with the character of the overlying Gametrail carbonates at Sekwi Brook, which are of ribbon-bedded facies, interrupted only by monomict, matrix-supported, debris-flow breccias and slide masses. Thus, in the Sekwi Brook area, southwestward-prograding slope deposits (upper Sheepbed, Gametrail) appear to have buried axially prograding deep-sea fan deposits (lower Sheepbed).

Blueflower Formation

The Blueflower Formation is not preserved above the Sheepbed and Gametrail formations of the 'typical' outcrop belt (Text-fig. 2). At Sekwi Brook it is 550 m thick, and consists of dark-coloured, deep-water shale and mudstone (59%), turbiditic sandstones (15%), and limestones of turbiditic and grain-flow origin (26%). It is the lower part of a shoaling-upward cycle that terminates with the peritidal dolomites of the overlying Risky Formation. Other upward trends within the Blueflower are: decrease and virtual disappearance of carbonate beds; increase in the proportion of sandstone; and the appearance, near the top, of non-turbiditic sandstones with low-angle cross-stratification.

Sandstones in the lower three-quarters of the formation are predominantly thin-bedded, fine-grained turbidites (Bouma Tb, Tc, and Tbc), with a few thicker and generally coarser beds that are Bouma Ta and Tab units, and structureless beds interpreted as liquefied-flow deposits (Lowe 1982). Flame structures are common, flute and groove casts less so. Thin sandstone beds are persistent across the typical widths of the gully outcrops (50 m), but bundles of such beds are markedly lenticular over distances of 200–400 m.

Limestones occur in packets of two types: ribbon-bedded lime mudstone, in part displaying flame structures and normal supply-grading of a sparse content of quartz sand grains; and subordinate, markedly lenticular packets of medium and thick beds of intraclast grainstone and wackestone with a variable content of quartz sand grains. Most of the latter display normal grading, and are Bouma Tab and Tb units. The packets of ribbon-bedded limestone are distinctly lenticular over distances of less than one kilometre.

Evidence of deposition on a slope is common. It includes penecontemporaneous folds, detached fold-noses in dismembered sandstone beds, scoop-shaped slide surfaces, contorted and mixed mudstone units with deformed pods of sandstone, matrix-supported debris-flow breccias, at least two slide masses or debris-flow paraconglomerates with boulders of shallow-water carbonate rocks, rare exotic blocks and boulders, and, high in the type section, an exotic raft of stromatolitic dolomite.

The overall aspect of the lower three-quarters of the Blueflower at Sekwi Brook is that of a slightly channelled slope below storm wave-base. The content of thin-bedded turbidites, with thickening-upward and less common thinning-upward sequences, might suggest the middle to lower parts of a deep-sea fan. Indeed, a lens of thick-bedded, massive sandstone cropping out less than one kilometre north of the type section resembles a fan-channel deposit. The abundant evidence of slope deposition is, however, inconsistent with a fan interpretation overall. Because it characterizes the middle and upper parts of the formation, it probably records a depositional slope prograding above a fan-complex.

Towards the top of the Blueflower Formation, carbonate rocks reappear as blocks, boulders and rafts of limestone and dolomite of shallow-water origin. These document the progradational approach of a re-established carbonate platform, the Risky Formation, which appears at a gradational contact.

Summary

Thus it is apparent that most of the Ediacaran fossils at Sekwi Brook occur in strata deposited in a deep-water, basin slope setting considerably below storm wave-base. This is in marked contrast with the shallow-shelf assemblages in the nearby Wernecke Mountains (Narbonne and Hofmann 1987). The occurrence of assemblages of shallow- and deep-water Ediacaran fossils in localities only 250 km apart, within a single depositional and structural province, permits analysis of their bathymetric affinities, without the palaeogeographic uncertainties inherent in comparisons between distant areas.

FOSSIL OCCURRENCE AND PRESERVATION

Fossils were collected from three sections (Text-fig. 1) in the Sekwi Brook structural panel (*sensu* Aitken 1989*a*). The stratigraphy and distribution of fossils in the two main sections, Sekwi Brook North and Sekwi Brook South, is shown in Text-figures 3 and 4. Sekwi Brook North contains the type sections of the Gametrail, Blueflower and Risky Formations (Aitken 1989*a*); Sekwi Brook South was one of the sections investigated during the 1979 visit of the PreCambrian–Cambrian Boundary Working Group (Fritz 1980), and is the section where Hofmann (1981) described the first Ediacaran fossils discovered in western North America. In addition to these two main sections, trace fossils were collected from the lower half of the Blueflower Formation (locality 29), and trace fossils and body fossils were collected from the upper half of the Blueflower Formation (locality 30) during reconnaissance investigation of the Majesty Pb–Zn–Ag Property (Text-figs 1 and 4).

Some of the collections were made from outcrop, but most were from very local float (frost-heaved but effectively untransported slabs). The only exception is the figured specimen of *Ediacaria* sp., which was in float that had slid a considerable distance downhill, but which was tied into the section on the basis of the unique lithology and the presence of a fragmentary specimen of the same taxon in the same lithology at locality 27. Float that could not be tied down definitely stratigraphically was not included in the study material. The type of collection at each locality is shown in Text-figure 3.

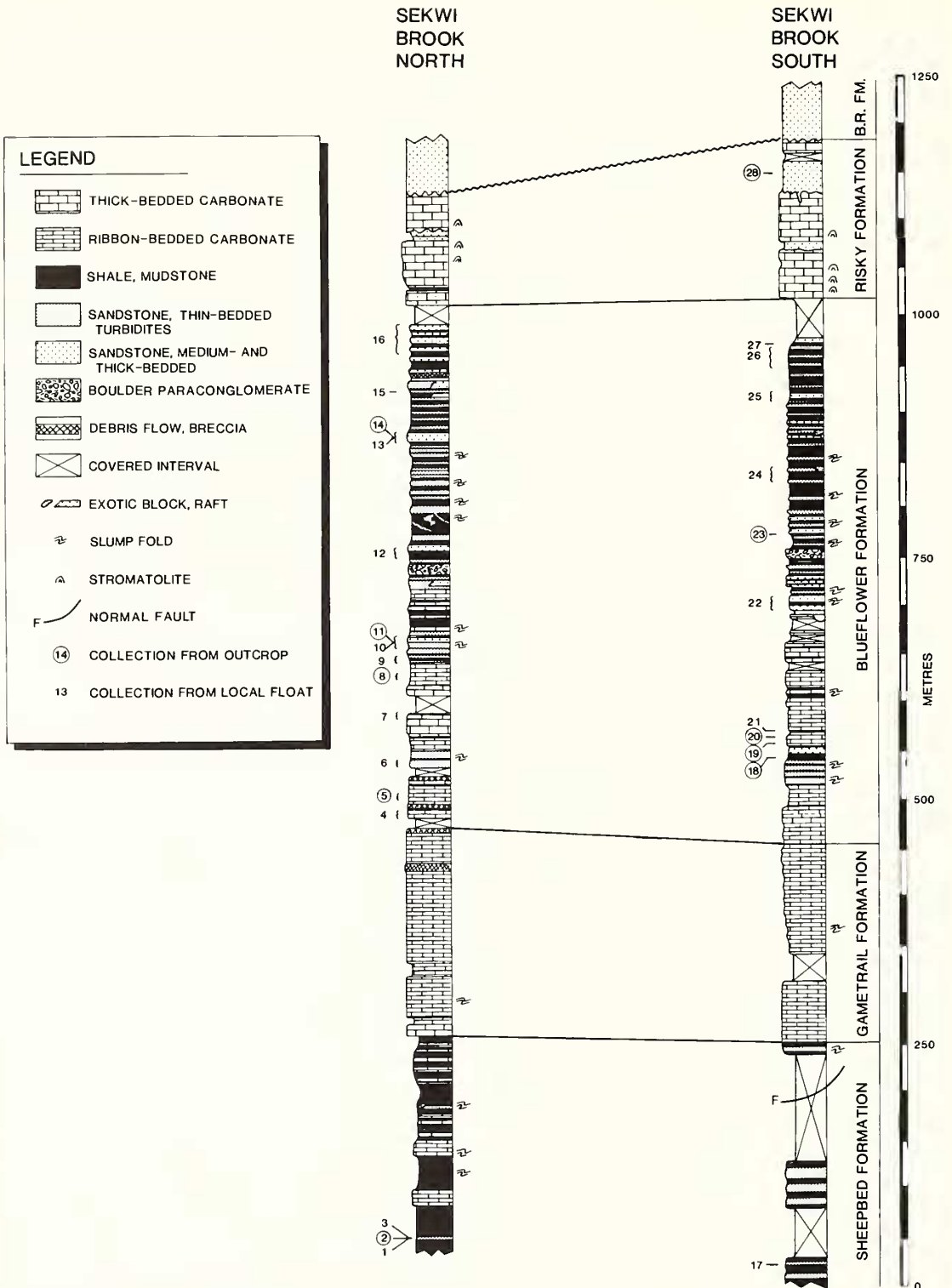
Ediacaran body fossils occur predominantly as raised features on the bottoms of beds (positive hyporelief) and very rarely as depressed features on soles (negative hyporelief). Trace fossils also exhibit the same modes of preservation, or occur as raised or depressed features on the tops of beds (positive/negative epirelief).

DISCUSSION

Body fossils

Previous reports of Ediacaran body fossils from the Sekwi Brook area by Hofmann (1981) and Aitken (1989*a*) were from the lower and middle parts of what is presently regarded as the Blueflower Formation. Our discoveries of specimens of *Charniodiscus* and *Ediacaria* near the top of this formation and of a relatively diverse assemblage of Ediacaran body fossils approximately 225 metres below the top of the Sheepbed Formation extends the known diversity and stratigraphic range of these fossils in the Mackenzie Mountains. Ediacaran body fossils have been reported by Narbonne and Hofmann (1987) from the 'Goz Siltstone' in the Wernecke Mountains, a unit tentatively correlated with the Sheepbed Formation (Narbonne *et al.* 1985), but the present paper represents the first confirmed report of an Ediacaran biota from the Sheepbed Formation. This is significant, as this unit is geographically widespread (Eisbacher 1981) and immediately overlies the highest Proterozoic glacial deposits in northwestern Canada (Aitken 1987, 1989*b*).

Ediacaran body fossils occur sporadically throughout approximately one kilometre of strata (upper Sheepbed Formation to the top of the Blueflower Formation) in the Sekwi Brook area of the Mackenzie Mountains. A total of ten genera comprising eleven species are now known from these strata (Text-fig. 4). The assemblage is broadly similar to that reported by Narbonne and Hofmann (1987) from equivalent strata in the Wernecke Mountains 250 kilometres to the west (Text-figs 5 and 6). Six genera (*Beltanella*, *Charniodiscus*?, *Cyclomedusa*, *Ediacaria*, *Kullingia*?, and *Medusinites*) are common to both areas. Six genera (*Beltanelliformis*, *Nadalina*, *Rugoconites*?, *Spriggia*, *Tirasiana*, and *Vendotaenia*?) are reported only from the Wernecke Mountains, and four genera (*Eoporpita*, *Inkrylovia*, *Pteridinium*, and *Sekwia*) are thus far known only from Sekwi Brook. Of the geographically restricted taxa, only *Beltanelliformis* is common, and the absence of the other



TEXT-FIG. 3. Stratigraphic sections and sample localities. B.R. FM. = Backbone Ranges Formation.

TAXA	STRATIGRAPHY			LOCALITIES																														
	Sheep-bed	Blue-flower	Risky	Sekwi Brook North						Sekwi Brook South						Majesty																		
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
BODY FOSSILS																																		
<i>Beltanella gilesi</i>																																		
<i>Charniodiscus?</i> sp.																																		
<i>Cyclomedusa plana</i>																																		
<i>Cyclomedusa</i> sp.																																		
<i>Ediacaria</i> sp.																																		
<i>Eoporpita</i> sp.																																		
<i>Inkrylovia</i> sp.																																		
<i>Kullingia?</i> sp.																																		
<i>Medusinites asteroides</i>																																		
<i>Pteridinium</i> sp.																																		
<i>Sekwia excentrica</i>																																		
Plumose problematicum																																		
ICHNOFOSSILS																																		
<i>Aulichnites</i> ichnosp.																																		
<i>Helminthoida</i> ichnosp.																																		
<i>Helminthoidichnites tenuis</i>																																		
<i>Helminthopsis abeli</i>																																		
<i>Helminthopsis irregularis</i>																																		
<i>Helminthopsis?</i> ichnosp.																																		
<i>Lockeia</i> ichnosp.																																		
<i>Neonereites?</i> ichnosp.																																		
<i>Palaeophycus tubularis</i>																																		
<i>Planolites montanus</i>																																		
<i>Torrowangea rosei</i>																																		
Knotted burrow																																		

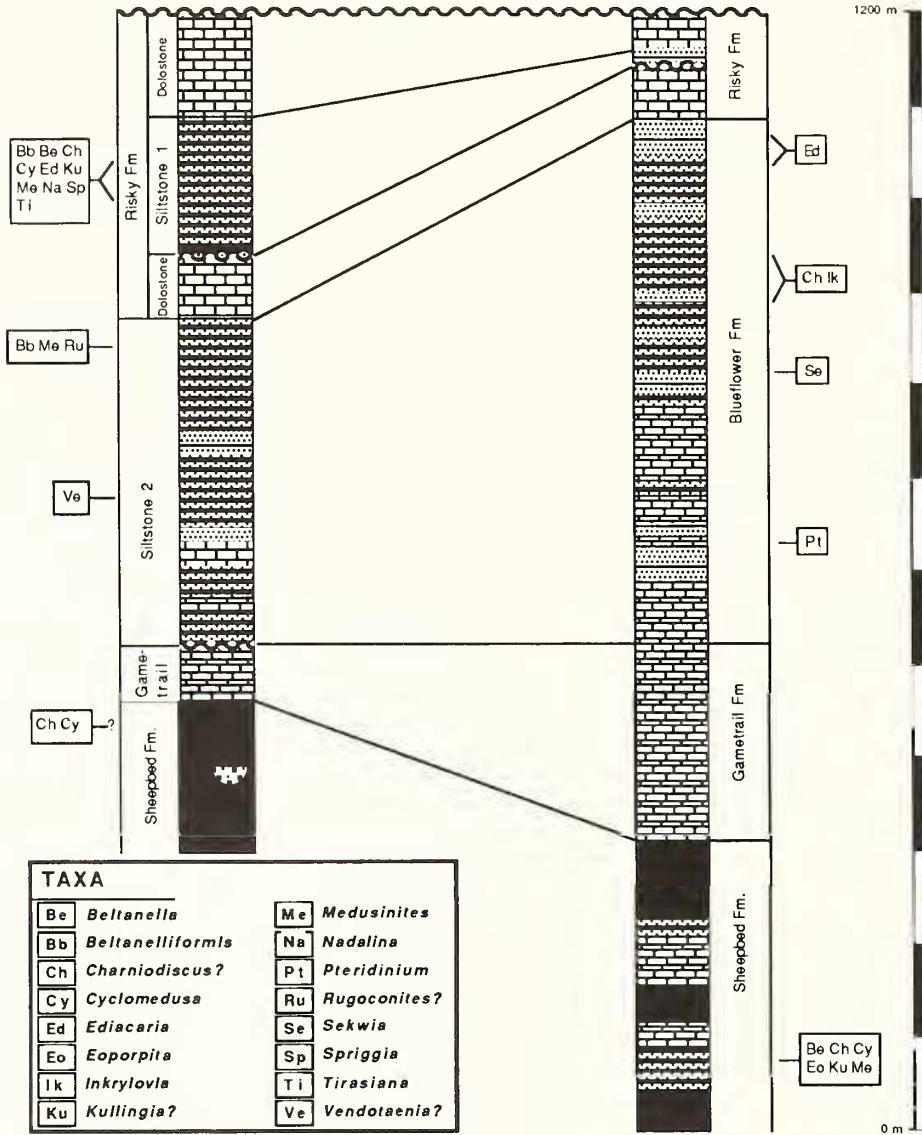
TEXT-FIG. 4. Synopsis of Ediacaran macrobiota from the Sekwi Brook region.

taxa may simply reflect the relatively short periods of time devoted to collecting in these remote regions. Thus, it would appear that the faunas from the Wernecke and Mackenzie Mountains can be regarded as part of a single 'Windermere fauna' that characterizes the Ediacaran of northwestern Canada, and may also include the low diversity fauna described by Hofmann *et al.* (1985) from the southern Canadian Rocky Mountains.

A tentative correlation of the formations and body fossils of the Wernecke and Mackenzie Mountains is shown in Text-figure 5. With the exception of the middle siliciclastic unit of the Risky Formation, which at Sekwi Brook consists entirely of thick-bedded dolomitic sandstone and thus represents an unfavourable facies for preservation, all units that contain Ediacaran fossils in the Wernecke Mountains have fossiliferous correlatives in the Mackenzie Mountains. However, fossil assemblages in correlative units are not particularly similar, and the greatest faunal similarity is between the youngest fossiliferous unit in the Wernecke Mountains and the oldest fossiliferous unit in the Mackenzie Mountains! This suggests that most of the apparent geographical and

CORN CREEK AREA,
WERNECKE MTNS

SEKWI BROOK AREA,
MACKENZIE MTNS



TAXA

Be <i>Beltanella</i>	Me <i>Medusinites</i>
Bb <i>Beltanelliformis</i>	Na <i>Nadalina</i>
Ch <i>Charniodiscus?</i>	Pt <i>Pteridinium</i>
Cy <i>Cyclomedusa</i>	Ru <i>Rugoconites?</i>
Ed <i>Ediacaria</i>	Se <i>Sekwia</i>
Eo <i>Eoporpita</i>	Sp <i>Spriggia</i>
Ik <i>Inkrylovia</i>	Ti <i>Tirasiana</i>
Ku <i>Kullingia?</i>	Ve <i>Vendotaenia?</i>

Lithology

ribbon-bedded carbonate	shale, with minor turbidite/storm sandstone beds
thick-bedded carbonate	medium-bedded sandstone
shale/mudstone	conglomeratic channel

TEXT-FIG. 5. Correlation of Ediacaran strata and megafossils in the eastern Werneck Mountains and in the Sekwi Brook area of the Mackenzie Mountains. Lithological correlations are from Aitken (1989a, fig. 7); faunal lists are from Narbonne and Hofmann (1987) and the present study.

stratigraphic variation in the Windermere fauna reflects palaeoenvironmental and preservational factors, and an original patchy distribution, rather than palaeogeography and evolution. This view is supported by the great variation in the faunal content of equivalent strata in adjacent sections (cf. Narbonne and Hofmann 1987, text-figs 2 and 3; this study, Text-figs 3 and 4), even where the sections are within sight of each other. For this reason, we believe that any attempt to subdivide the Windermere fauna into biostratigraphic zones would be premature at the present time.

Global correlation of the Windermere body fossils is summarized in Text-figure 6. Close similarities are evident between the faunas of the Wernecke and Mackenzie Mountains, the Ediacara Member of the Rawnsley Quartzite in South Australia, and the Redkino 'Series' of the Vendian in northern Europe and Podolia. The Windermere biota is considerably less diverse than those reported from the other two regions, and apparently lacks segmented forms such as *Spriggina* and *Dickinsonia*, which are present in South Australia and on the Russian Platform. This may relate to the relatively early stages of investigation in northwestern Canada, a palaeogeographic separation between Laurentia and the latter-mentioned two areas (see McMenamin and McMenamin 1990), or some other palaeoecological or stratigraphic factor. Nevertheless, the high proportion of Windermere taxa that are also known from the type Ediacaran and the type Vendian (Text-fig. 6), emphasizes the considerable correlation potential of the Ediacaran fauna.

Baudet *et al.* (1989) concluded that the acritarchs of the Sheepbed and Blueflower Formations best correlate with the Kotlin 'Series' of the Vendian on the Russian Platform. This contradicts the above correlation, as the macrofossils of these formations are much more similar to the fossil assemblage of the Redkino 'Series' (see above) than they are to those of the overlying Kotlin 'Series', which lacks identifiable megafossils (Sokolov and Fedonkin 1984). The stratigraphic setting of these units, immediately overlying a diamictite unit and two or more Grand Cycles (400–1200 m) below the lowest Cambrian-type fossils (*Phycodes pedum* Zone), is also quite similar to that of the Redkino 'Series' and supports the correlation based on macrofossils. On the basis of published descriptions of the body fossils, ichnofossils, small shelly fossils, and the overall stratigraphic sequence, Narbonne *et al.* (1987, fig. 8) concluded that the probable equivalents of the Kotlin 'Series' in the Mackenzie Mountains are the upper part of the Risky Formation and the overlying Ingta Formation. Baudet *et al.* (1989) were unable to date these latter units, as they did not yield diagnostic acritarchs in their study. Thus, the majority of the evidence suggests that the Sheepbed, Gametrail, Blueflower and lower Risky Formations are equivalent to the Redkino 'Series' of the Vendian, and that the upper Risky and Ingta formations are equivalent to the Kotlin 'Series'.

Until recently, it was generally believed that the Ediacaran fauna was dominated by discoidal pelagic medusoids (e.g. Sprigg 1947, 1949; Glaessner and Wade 1966). Fedonkin (1985a) and Jenkins (1988) have reinterpreted many of the forms as benthic 'polyps', and this interpretation also seems to be appropriate to the Windermere biota. With the possible exception of *Kullingia*?, the fauna is entirely dominated by benthic organisms, both in terms of numbers and diversity (see Systematic Palaeontology below). The shapes of many Ediacaran organisms and their common occurrence in shallow-water facies has led some authors to suggest that they may have been partly or completely photoautotrophic (e.g. McMenamin 1986), but this is not consistent with their occurrence in muddy slope deposits considerably below storm wave-base in the Sekwi Brook area.

The Sekwi Brook fauna represents the first report of an Ediacaran assemblage in a basin slope setting. The Sekwi Brook fauna is markedly different from those reported from the deep slope/fan 'Avalon assemblage' of Newfoundland (e.g. Anderson and Conway Morris 1982), Charnwood Forest (e.g. Ford 1980), and the Carolina Slate Belt (Gibson *et al.* 1984), with only two or three of the reputedly more than twenty forms from these settings also present at Sekwi Brook. It is presently uncertain how much of this difference is palaeoenvironmental, and how much reflects palaeogeography. A closer similarity exists between the basin slope faunas from Sekwi Brook and those reported from shallow shelf deposits in the Wernecke Mountains, Flinders Ranges, Podolia, northern Europe and elsewhere (Text-fig. 6). This implies that some elements of the Ediacaran fauna extended over a considerable depth range.

TAXA	NORTHWESTERN CANADA		GLOBAL COMPARISONS											
	SHALLOW SHELF	BASIN SLOPE	SHALLOW SHELF						DEEP SLOPE/FAN					
	Wernecke Mtns.	Sekwi Brook	VENDIAN			EDIACARAN			OTHERS					
			Northern Europe	Podolia	Urals	Siberia	Flinders Ranges	Central Australia	Namibia	Central England	North Carolina			
BODY FOSSILS	<i>Beltanella</i>													
	<i>Beltanelliformis</i>	▬		□	□	□	□	○	○	□				
	<i>Charniodiscus?</i>		□		□		□	□	□		□			
	<i>Cyclomedusa</i>	▬	□	□		□			□		○			
	<i>Ediacaria</i>		□	□				□						
	<i>Eoporpita</i>		□					□						
	<i>Inkrylovia</i>		□											
	<i>Kullingia?</i>		□	□		□			○					
	<i>Medusinites</i>		□	□		○		□						
	<i>Nadalina</i>													
	<i>Pteridinium</i>		□	□				□		□				□
	<i>Rugoconites?</i>							□						
	<i>Sekwia</i>													
	<i>Spriggia</i>							□						
	<i>Tirasiana</i>				□	□					○			
<i>Vendotaenia?</i>			○	○		○								
ICHOFOSSILS	<i>Aulichnites</i>			□										
	<i>Helminthoida</i>			□					○					
	<i>Helminthoidichnites</i>		▬	□	□				□					□
	<i>Helminthopsis</i>		▬											□
	<i>Lockeia</i>													
	<i>Neonereltes?</i>			□	□				○					□
	<i>Palaeophycus</i>													□
	<i>Planolites</i>		▬	□	□				□	□	□			□
	<i>Torrowangea</i>			□										○

TEXT-FIG. 6. Regional and global correlation of the Windermere biota. Localities with less than two Windermere-type taxa are omitted. Abundance symbols for northwestern Canada: narrow bar = rare (present in < 10% of fossiliferous units); intermediate bar = common (present in 10–50% of fossiliferous units); broad bar = abundant (present in > 50% of fossiliferous units). For global comparisons, same (square) or similar (circle) forms indicated.

Ichnofossils

A relatively diverse assemblage of trace fossils is present in the Ediacaran strata of the Sekwi Brook area (Text-figs 4 and 6). Previously, the oldest known trace fossils in northwestern Canada were

from the Blueflower Formation (Hofmann 1981; Aitken 1989a) and its stratigraphic equivalent in the Wernecke Mountains (Narbonne and Hofmann 1987). The occurrence of specimens of *Planolites montanus* in the upper part of the Sheepbed Formation extends the stratigraphic range of trace fossils downwards by approximately 500 metres. The Blueflower Formation contains a more diverse assemblage of trace fossils, comprising at least twelve ichnospecies referable to nine ichnogenera. All taxa known from the Ediacaran of Sekwi Brook also range the Phanerozoic. Forms restricted to the Ediacaran (e.g. *Harlaniella*, *Palaeopascichmus*, *Nenoxites*, etc.) have not yet been documented from Sekwi Brook.

Seilacher (1964, 1967) first suggested that trace fossils show a consistent ecological zonation throughout the Phanerozoic which he subdivided into several 'universal ichnofacies'. Although numerous studies have supported and refined Seilacher's model (see Ekdale *et al.* 1984 and references therein), it remains uncertain when and how ichnofacies first developed. Most of the ichnotaxa at Sekwi Brook also occur in shallower water deposits in the Ediacaran of the Wernecke Mountains, eastern and northern Europe, and Australia, and in deep slope/fan deposits in the Carolina Slate Belt (Text-fig. 6). This supports the view of Crimes and Anderson (1985) that upper Precambrian-Lower Cambrian trace fossil assemblages show a lower degree of palaeo-environmental differentiation than do those in post-Cambrian strata.

Basin slope deposits at Sekwi Brook also contain abundant simple burrows (e.g. *Planolites* and *Palaeophycus*), and non-directed meanders (especially *Torrowangea* and *Helminthoidichnites*); patterned meanders occur rarely (*Helminthoida*) to commonly (*Helminthopsis*). The presence of an assemblage dominated by meandering forms and apparently lacking vertical burrows and arthropod traces is reminiscent of the *Nereites* ichnofacies of Seilacher (1964, 1967). The *Nereites* ichnofacies typifies turbiditic slope deposits of Phanerozoic age but had not previously been reported from the Precambrian. The comparatively low diversity, the apparent absence of graphoglyptids, and the dominance of unpatterned and simple patterned forms among the meandering burrows of the Blueflower (basin slope) assemblage implies that this Precambrian assemblage represents a relatively simple version of the ichnofacies, and is consistent with Seilacher's (1974, 1977) observation that the *Nereites* ichnofacies exhibits a step-wise increase in all three of these features throughout the Phanerozoic. Previous evolutionary models for trace fossils (e.g. Crimes 1974; Seilacher 1974, 1977; Frey and Seilacher 1980) have generally concluded that deep-water slopes of Ediacaran/Vendian age were all but completely devoid of infaunal animal life, but the new evidence from the Carolina Slate Belt (Gibson 1989), the Avalon Zone of Newfoundland (pers. comm. M. M. Anderson 1989) and the Sekwi Brook area (this study) indicates that the initial radiation of metazoans also extended to the sediments of the deep-sea.

Previous workers (e.g. Crimes and Anderson 1985) suggested that complexly meandering burrowers first evolved in shallow-water settings in the early Cambrian, and later migrated into deeper-water settings. It now appears more likely that meandering burrowers originated in the Precambrian, where they occurred in both shallow marine (Glaessner 1969; Fedonkin 1985c) and deep marine (this study) settings. The explosive diversification of shallow-water burrowers in the early Cambrian, including the first appearance of abundant complexly branching, spreiten-bearing, and deep vertical burrows (cf. Alpert 1977; Crimes 1987; Narbonne *et al.* 1987), gradually eliminated meandering burrowers, especially forms producing complex meanders, from shallow-water settings. However, a low diversity assemblage of meandering burrows persisted in deeper-water slope settings, and gradually increased in diversity and burrow complexity throughout the remainder of the Phanerozoic.

SYSTEMATIC PALAEOONTOLOGY

Although genus- and species-level identification of Ediacaran organisms are relatively stable, no classification of family and higher taxonomic levels has yet been accepted. Conway Morris (1985) has argued that attempts to relate Ediacaran organisms to extant phyla and classes may obscure the relationships among these early metazoans, and even the assignment of some Ediacaran fossils to

the Metazoa has been questioned by Seilacher (1984, 1989). Rival classification schemes are presented in Pflug (1972), Glaessner (1979), Seilacher (1989), Fedonkin (1985*b*), Gureev (1987) and other papers. A full evaluation of these proposals is beyond the scope of this study, and the Sekwi Brook fossils are simply classified as 'body fossils' or 'ichnofossils' (= trace fossils). Dubiofossils have been described by Hofmann (1981), and are not included in the present study. Acritarchs from these strata have also been discussed previously (Baudet *et al.* 1989).

In the following section, synonymies include only Precambrian forms; the occurrence (if any) of Cambrian or younger forms is discussed under 'Remarks'. All type and figured specimens have been deposited in the National Type Collection of Invertebrates and Plants, Geological Survey of Canada (GSC) in Ottawa, Canada.

BODY FOSSILS

Genus BELTANELLA Sprigg, 1947

Type species. Beltanella gilesi Sprigg, 1947.

Beltanella gilesi

Plate 1, fig. 1

For synonymy up to 1987, see Narbonne and Hofmann (1987).

1987 *Beltanella gilesi* Narbonne and Hofmann, pp. 653–654, pl. 73, fig. 6.

1987 *Planomedusites grandis* Gureev, pp. 40–42, fig. 16.

Description. Single incomplete disc preserved in convex hyporelief. Smooth disc 40 mm in diameter with a prominent central tubercle 4.8 mm in diameter; disc surrounded by a flange 5–11 mm wide with irregularly spaced marginal indentations. Poorly preserved, tapering stalk 20 mm wide at its base extending 40 mm beyond the outer edge of the flange.

Remarks. The specimen is strikingly similar to one illustrated by Narbonne and Hofmann (1987, pl. 73, fig. 6) from the Wernecke Mountains of northwestern Canada. *Beltanella* has traditionally been interpreted as a pelagic medusoid (e.g. Sprigg 1947; Harrington and Moore 1956), but Jenkins (1988) recently reinterpreted it as a benthic polyp attached to the sea-bottom by a short stalk. The specimen of *Beltanella* from Sekwi Brook exhibits a poorly preserved stalk which extends outward from the outer margin of the disc, thereby implying that it was above rather than below the disc. As this structure is known from a single specimen, it is uncertain whether or not it is accidental.

Genus CHARNIODISCUS Ford, 1958

Type species. Charniodiscus concentricus Ford, 1958

EXPLANATION OF PLATE 1

Fig. 1. *Beltanella gilesi* Sprigg, hyporelief. Locality 17, Sekwi Brook South, GSC 95895, $\times 1$.

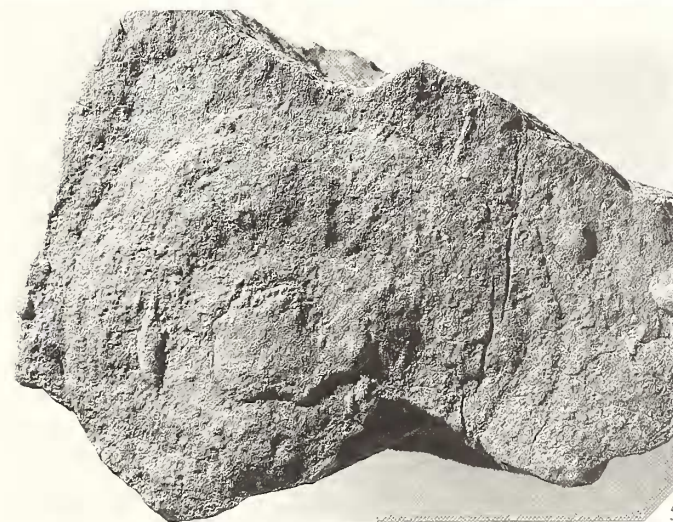
Figs 2 and 6. *Cyclomedusa* sp., hyporelief. 2, locality 3, Sekwi Brook North, GSC 95896, $\times 1$. 6, three specimens that interfered with each other during growth, locality 17, Sekwi Brook South, GSC 95898–95900 (clockwise from top right), $\times 1$.

Fig. 3. Plumose problematicum, epirelief. Locality 3, Sekwi Brook North, GSC 95897, $\times 1.5$.

Fig. 4. *Cyclomedusa plana* Glaessner and Wade, hyporelief. Locality 3, Sekwi Brook North, GSC 95902, $\times 1.5$.

Fig. 5. *Ediacaria* sp., hyporelief. Float, probably from locality 27, Sekwi Brook South, GSC 95903, $\times 0.5$.

Fig. 7. *Charniodiscus?* sp., hyporelief. Locality 30, Majesty Section, GSC 95904, $\times 1$.



Charniodiscus? sp.

Plate 1, fig. 7

Description. Five circular discs preserved in positive hyporelief (0.5–2.5 mm relief). Central tubercle 3–8 mm in diameter surrounded by 3–5 concentric rugae. Disc diameter 26–46 mm (mean = 37.2 mm). Gently tapering stalk, 12–21 mm wide at its base, extending up to 85 mm from the outer margin of the disc.

Remarks. Ford (1958) originally described *Charniodiscus* on the basis of a single concentric disc with an attached stalk, and later (1963) figured the complete specimen with a frond attached to the stalk. Jenkins and Gehling (1978) and Glaessner (1979) subsequently regarded the frond as the most diagnostic part of the fossil. The absence of an attached frond in any of the Sekwi Brook specimens thus far collected precludes more specific identification. Two specimens of the frond of *Charniodiscus* cf. *arboreus* and numerous basal discs of *Charniodiscus?* were described from the Wernecke Mountains by Narbonne and Hofmann (1987, fig. 5c).

Genus CYCLOMEDUSA Sprigg, 1947

Type species. *Cyclomedusa davidi* Sprigg, 1947.

Cyclomedusa plana Glaessner and Wade, 1966

Plate 1, fig. 4

For synonymy to 1987, see Narbonne and Hofmann (1987).

1987 *Cyclomedusa plana* Narbonne and Hofmann, pp. 656–658, pl. 73, fig. 3.

1987 *Glaessneria plana* Gureev, fig. 14.

1987 *Glaessneria imperfecta* Gureev, p. 40, fig. 15.

Description. Two bipartite discs preserved in convex hyporelief. Central cone (5.2 mm relief) or concentrically-ringed disc (< 0.5 mm relief) 5.1–7.1 mm in diameter superimposed on a flat disc approximately 34 mm in diameter. Outer edge of the fossil exhibiting a sharp annulus 0.8–1.2 mm wide and 0.5 mm high. Surface of the outer disc smooth, or marked by very fine radial grooves.

Remarks. The status of *C. plana* is controversial. Until recently, most authors have followed Glaessner and Wade (1966), and regarded it as a species of *Cyclomedusa*. Sun (1986) questioned whether *C. plana* should be included in *Cyclomedusa*, as it is poorly understood and exhibits some significant differences with the type species. Gureev (1987) specifically removed *C. plana* from *Cyclomedusa*, and regarded it as the type species of his new genus *Glaessneria*. Alternatively, Jenkins (1988, 1989) has pointed out that *Cyclomedusa* and other discoid Ediacaran genera have been oversplit, and that there is evidence of intergradation among some of the species of the *Cyclomedusa* plexus and perhaps even among some related genera. Further systematic revision of *Cyclomedusa* is obviously needed, but in the interim we follow Glaessner and Wade (1966) in regarding *C. plana* as a valid species of *Cyclomedusa*.

Most figured specimens of *C. plana*, including material from the Wernecke Mountains (Narbonne and Hofmann 1987) and from Sekwi Brook (e.g. GSC 95901), exhibit a series of concentric wrinkles near the centre of the disc; this presumably represents a conical apex that was folded flat during compaction. One specimen from Sekwi Brook (Pl. 1, fig. 4) resembles two unfigured specimens from South Australia (collected in 1988 and now in the collections of R. J. F. Jenkins) in exhibiting an uncompressed cone at its apex. This implies that the cone was buried in relatively cohesive mud while the flat outer ring rested on the sea floor.

Cyclomedusa plana is a cosmopolitan taxon (Wade 1972), not known from Australia, eastern Europe and western North America (see synonymy in this paper and in Narbonne and Hofmann 1987).

Cyclomedusa sp.

Plate 1, figs 2 and 6; Plate 2, figs 3 and 5

Description. Twenty-one measured specimens and numerous field identifications, all preserved in positive hyporelief. Circular discs 13.4–58.5 mm (mean = 26.2 mm) in diameter with central tubercle, 1.1–7.7 mm; tubercle surrounded by irregularly-spaced concentric markings. Very fine radial ridges locally present (e.g. Pl. 1, fig. 2; Pl. 2, fig. 5). Relief 0.3–3.5 mm, with maximum relief in centre. Specimens deformed laterally where in contact (Pl. 1, fig. 6).

Remarks. Specimens are mostly at the small end of the size range for *Cyclomedusa*, which has a maximum diameter of more than 100 mm (Sun 1986). They closely resemble the specimens illustrated by Wade (1972, pl. 41, fig. 1) as *C. davidi* Sprigg, and like them show evidence that they were originally highly conical. Sun (1986) questioned whether these specimens should be included in *C. davidi* as the radial striations typical of this species are not well developed in Wade's specimens, an objection that applies equally well to the specimens from Sekwi Brook and elsewhere in northwestern Canada (Narbonne and Hofmann 1987). However, the presence of fine radial striae on the bases of *Cyclomedusa* specimens has been attributed by Sun (1986) to composite molding of features on the oral and aboral surfaces. Composite molding is prevalent in the Flinders Ranges but is relatively rare in most other Ediacaran deposits, and it would seem unwise to base a generic difference on a preservational feature. Further systematic revision of *Cyclomedusa* is obviously needed, but in the interim we refer these specimens to *Cyclomedusa* sp.

The interpretation of discoid Ediacaran fossils such as *Cyclomedusa* is uncertain, with various authors regarding them as impressions of pelagic medusae (e.g. Wade 1968; Sun 1986), benthic polyps (e.g. Fedonkin 1985a; Jenkins 1988), sea-pen attachment structures (Jenkins 1989), or burrows similar to those produced by modern actinians (Seilacher 1984). The absence of specimens preserving the oral surface among any of the specimens from northwestern Canada is not consistent with the orientations of medusae stranded at the strand line or in deeper water (cf. Wade 1968). This implies that the aboral surface permanently rested on or in the substrate, and thus that the *Cyclomedusa* organism was benthic. Closely-crowded specimens on the same bedding plane tend to be relatively similar in size (e.g. Hofmann *et al.* 1983, fig. 2A; Narbonne and Hofmann 1987, text-fig. 5a; this study, Pl. 1, fig. 6), and may represent products of a single spatfall. The fact that closely-crowded specimens deform but do not cross-cut each other, and evidence of increasing mutual deformation during growth (Pl. 1, fig. 6), support the interpretation of *Cyclomedusa* sp. as the impression of a sessile benthic organism. Most likely, the prominent central tubercle represents the point where the pelagic larva settled onto the bottom and dug a small pit for attachment to the sea floor. The organism was firm-bodied, and apparently grew out concentrically in the shape of a cone. With the possible exception of the central tubercle there is no evidence of active burrowing; however passive sedimentation of mud around the bases of some of the cones may have resulted in the relatively high relief of some specimens (e.g. Pl. 1, figs 2 and 6). The organism was later buried by a sandy turbidite or storm bed, and was cast by the subsequent collapse of the sand into the space formerly occupied by the organism.

This model implies that *Cyclomedusa* sp. and perhaps other Ediacaran discs with a prominent central tubercle, represent impressions of firm-bodied organisms that were sessile except during their larval stages. The nature of the oral surface remains uncertain, with various authors showing evidence for tentacles (Wade 1972, pl. 41, fig. 2) or stalks (Jenkins 1989, fig. 2E) in some specimens. Elucidation of this is important, as *Cyclomedusa* is one of the most widely recognized Ediacaran fossils.

Genus EDIACARIA Sprigg, 1947

Type species. *Ediacaria flindersi* Sprigg, 1947.

Ediacaria sp.

Plate 1, fig. 5

Description. One nearly complete specimen and one fragment, both preserved in positive hyporelief. Complete specimen a slightly elliptical bipartite disc, 160–170 mm in diameter. Central disc 110–120 mm in diameter, with concentric grooves and discontinuous radial ridges particularly well-developed towards its periphery. Poorly preserved outer flange 25 mm wide, marked by irregular texture and discontinuous radial ridges. Maximum relief of 1.5 mm in the central disc. Possible central circular depression 25 mm in diameter largely covered by sediment.

Remarks. The large size and bipartite to tripartite organization are typical of *Ediacaria*, but the relatively poor quality of preservation does not permit definite comparison with *E. flindersi*, the only named species of this genus. *Ediacaria*, the largest discoid fossil of the Ediacara assemblage, was previously interpreted as a 'medusoid' (Sprigg 1947; Glaessner and Wade 1966) but Fedonkin (1985a) and Jenkins (1988, 1989) have reinterpreted it as an attached polyp.

Genus *EOPORPITA* Wade, 1972

Type species. *Eoporpita medusa* Wade, 1972

Eoporpita sp.

Plate 2, fig. 1; Plate 3, fig. 4

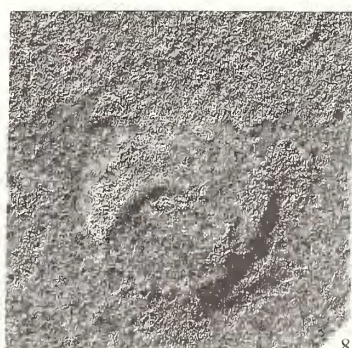
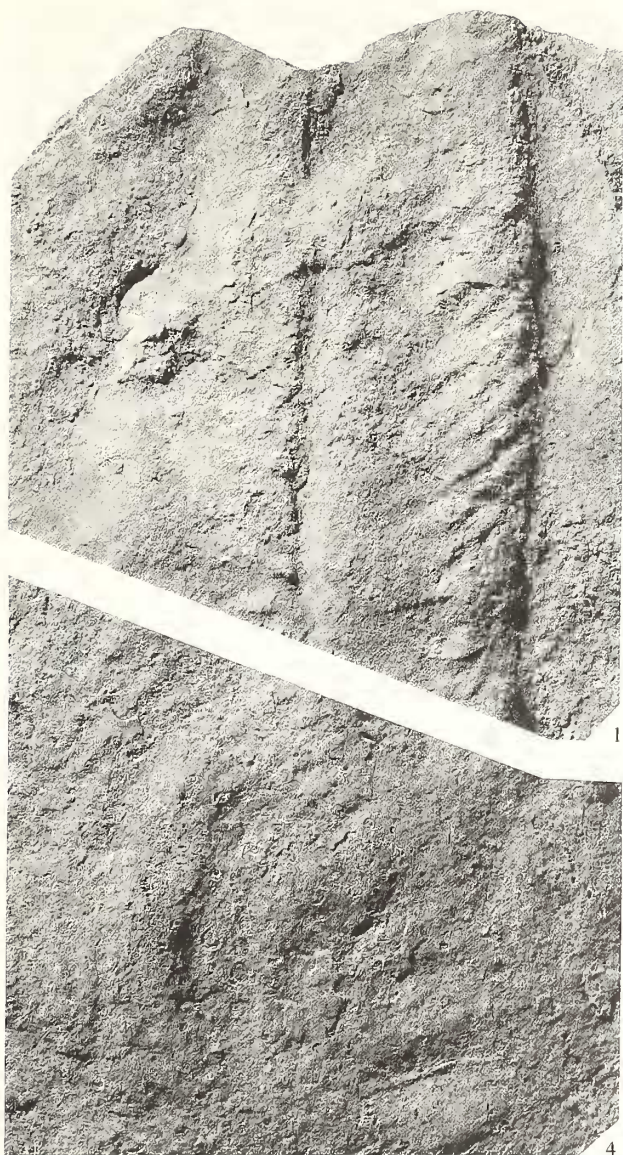
Description. Three discoid specimens preserved in positive hyporelief. Bipartite central cup consisting of a conical knob 4.9–7.1 mm in diameter and 2.1–4.5 mm high surrounded by an upwards-flaring flange 9.2–13.0 mm in diameter and 1.3–1.8 mm high; surface of the flange covered with approximately 12–24 hemispherical to radially elongate pustules 1.5–2.5 mm wide. Flange surrounded by a radiating pattern of approximately twenty-five club-shaped tubes 2.1–4.2 mm wide passing off the pustules and extending outwards to the margin of the fossil. Tubes predominantly straight to slightly sinuous, but locally strongly curved. Total fossil diameter 30–66 mm.

Remarks. The two specimens illustrated in Plate 3, fig. 4 are approximately 25% smaller than the smallest specimens reported by Wade (1972), but the largest specimen is well within the described range of variation of *Eoporpita*. The central cone, radially elongate pustules, and radiating clavate tubes are all diagnostic of *Eoporpita*. However, in contrast with *E. medusa* Wade, which exhibits overlapping whorls of tubes, the Sekwi Brook specimens exhibit only an incipient overlapping near the central zone. For this reason, we refer our material to *Eoporpita* sp.

Wade (1972) originally interpreted *Eoporpita* as a primitive chondrophorian with a chambered float (pneumatophore) and whorls of radiating tentacles, a view supported by most subsequent workers (e.g. Glaessner 1979; Stanley 1986). According to this interpretation, the Sekwi Brook specimens would reflect preservation of the oral surface; the central cone, elongate pustules, and

EXPLANATION OF PLATE 2

- Fig. 1. *Eoporpita* sp., hyporelief. One kilometre north of locality 3, Sekwi Brook North, GSC 95905, $\times 1$.
 Fig. 2. *Pteridinum* sp., hyporelief. Locality 18, Sekwi Brook South, GSC 68463, $\times 1$.
 Figs 3 and 5. *Cyclomedusa* sp., hyporelief. Locality 3, Sekwi Brook North, 3, GSC 95907, $\times 1$. 5, GSC 95908, $\times 1$.
 Fig. 4. *Kullingia?* sp., hyporelief. Locality 3, Sekwi Brook North, GSC 95909, $\times 1$.
 Figs 6 and 7. *Medusinites asteroides* (Sprigg), hyporelief. 6, Locality 2, Sekwi Brook North, GSC 95910, $\times 2$.
 7, Locality 3, Sekwi Brook North, GSC 95911, $\times 2$.
 Fig. 8. *Sekwi excentrica* Hofmann, hyporelief. Locality 23, Sekwi Brook South, GSC 95912, $\times 2$.



clavate tubes would respectively represent the gastrozoid, incipient (gonozoid) tentacles and outer (dactylozoid) tentacles. However, experimental taphonomic studies led Norris (1989) to conclude that fossil chondrophorians are very unlikely to preserve a pattern of tentacles similar to that shown by *Eoporpita*. Evidence that the tubes were originally pliable can be seen in GSC 95916, where three of the tubes are deflected against the margin of a large, unidentified discoid fossil, but their original function remains uncertain.

Eoporpita is also known from the Flinders Ranges in Australia and from the White Sea region of the Russian Platform, but had not previously been reported from North America.

Genus KULLINGIA Glaessner in Føyn and Glaessner, 1979

Type species. *Kullingia concentrica* Glaessner in Føyn and Glaessner, 1979.

Kullingia? sp.

Plate 2, fig. 4

Description. One incomplete disc, partially overlying an indeterminate (?) stalked organism, preserved in convex hyporelief. Disc 160 mm in diameter and less than 1 mm in relief, marked by concentric ridges uniformly spaced 4 mm apart.

Remarks. The specimen is similar in size and morphology to the type species, *K. concentrica*, differing mainly in the wider spacing between concentric ridges. Føyn and Glaessner (1979) pointed out the similarity between the chambered structure of *Kullingia* and the concentrically-chambered float (pneumatophore) of a chondrophorian cnidarian. Alternatively, Seilacher (1984, 1989) suggested that some chambered Ediacaran discs may represent sedentary, benthic 'quasi-autotrophs' that were segmented to facilitate metabolic processes. Close similarity in morphology between Ediacaran, Palaeozoic, and modern chondrophorians supports the view that they are related (Stanley 1986; Narbonne *et al.* 1990).

Genus MEDUSINITES Glaessner and Wade, 1966

Type species. *Medusina asteroides* Sprigg, 1949.

Medusinites asteroides (Sprigg), 1949

Plate 2, figs 6 and 7

For synonymy up to 1987, see Narbonne and Hofmann (1987).

1987 *Medusinites asteroides* Narbonne and Hofmann, p. 660, pl. 73, figs 7–9

1987 *Medusinites asteroides* Gureev, pp. 30–31, fig. 10.

Description. Nine bipartite discs preserved in convex hyporelief. Smooth outer ring 13.4–24.8 mm (mean 18.7 mm) in diameter and less than 1.5 mm high with an incomplete outer flange 0.2–1.2 mm wide preserved on some specimens. Smooth inner disc 4.2–12.4 mm (mean 7.0 mm) in diameter and 0.5–2.1 mm high separated from outer ring by a sharp annulus. Diameter of the inner disc one quarter of one half of total diameter of the fossil. Fossil surface generally smooth, locally with very faint radial ridges and/or grooves on the outer ring.

Remarks. Specimens closely resemble those described by Glaessner and Wade (1966, pl. 97, figs 1 and 2) from Ediacara and by Narbonne and Hofmann (1987, pl. 73, figs 7–9) from the Wernecke Mountains. Sprigg (1949) and Glaessner and Wade (1966) regarded *Medusinites* as the impression of a medusoid. Alternatively, Fedonkin (1985a) interpreted *Paliella*, a very similar form possibly synonymous with *Medusinites* (Narbonne and Hofmann 1987), as a benthic 'polyp'. The absence

of specimens that preserve the oral surface suggests that *Medusinites* represents the base of a sedentary organism which lived with its mouth facing upwards. This is supported by the relatively high relief of some specimens, which implies that their bases were already buried in the mud at the time of sand deposition.

Genus PTERIDINIUM Gürich, 1933

Type species. Pteridinium simplex Gürich, 1933.

Pteridinium sp.

Plate 2, fig. 2

Description. One specimen figured by Aitken (1989a, fig. 6A) but not previously described; the scale bar on Aitken's figure is incorrect, and should read 3.75 cm. Specimen at least 92 mm long (incomplete at both ends), 60–62 mm wide, and with 4.5 mm of relief. Straight, smooth ribs 3.5–4 mm wide passing laterally from median furrow (V -angle = 100–120°) to the margin of the fossil. No evidence of a third vane.

Remarks. Pflug (1970) interpreted *Pteridinium* as a three-vaned, leaf-like structure. Distortion of these flexible organisms led to the wide range in morphology evident in *Pteridinium* (cf. Richter 1955; Glaessner and Wade 1966; Pflug 1970; Fedonkin 1981), a problem which hinders the recognition of species and comparisons with related forms such as *Inkrylovia*. *Pteridinium* was a cosmopolitan taxon that occurred over a broad bathymetric range (Gibson *et al.* 1984). The specimen from Sekwi Brook South in the first Ediacaran body fossil reported from deep-water carbonates.

Genus SEKWIA Hofmann, 1981

Type species. Sekwia excentrica Hofmann, 1981.

Sekwia excentrica Hofmann, 1981

Plate 2, fig. 8

1981 *Sekwia excentrica* Hofmann, pp. 305–307, fig. 4A–G.

Remarks. *Sekwia* was originally defined by Hofmann (1981) on the basis of twenty-four specimens collected from strata now assigned to the middle part of the Blueflower Formation at Sekwi Brook South. Our fieldwork in 1988 resulted in the discovery of two additional specimens from the same bed. Both specimens are well within the range of variation described by Hofmann (1981).

Sekwia excentrica is similar in size and eccentricity to the laterally deformed specimens of *Cyclomedusa* sp. (Pl. 1, fig. 7; Wade 1972, pl. 41, fig. 1) and *Sekwia kaptarenkoe* Gureev, 1987, but exhibits much lower relief and apparently lacks a central tubercle. One high-relief specimen questionably identified as *Sekwia* by Hofmann (1981, fig. 4H) was later referred to *Beltanelliformis* by Narbonne and Hofmann (1987). Re-examination of this specimen by the present authors suggests that it represents an indeterminate fossil that has been badly deformed by loading, and cannot definitely be ascribed to either of these genera.

Sekwia probably represents the impression of a highly conical cnidarian (Hofmann 1981), most likely a 'poly' similar in some respects to *Cyclomedusa* sp., that was flattened and deformed laterally during burial.

Plumose Problematicum

Plate 1, fig. 3

Description. One incomplete specimen preserved in negative hyporelief. Preserved length 51 mm, with a

maximum relief of 2.3 mm. Specimen petaloid, with a sharp outer margin. Plumose arrangement of sharp ridges 1–2.5 mm wide and up to 1.4 mm high extending the length of the specimen.

Remarks. The specimen superficially resembles tectonic features such as plumose fractures, but this is ruled out by the presence of a thin carbonaceous lamella that evenly covers the entire bedding surface, including the sides and tops of the fine ridges. This indicates that they represent very sharp folds of the bedding surface (prelithification) rather than tectonic fractures of the rock surface (postlithification). The presence of a sharp outer margin is also atypical of plumose fractures. Preservation of the structure in negative hyporelief, and the occurrence of undeformed specimens of indeterminate discoid megafossils preserved in positive hyporelief elsewhere on the same slab (GSC 95906), both imply that the structure does not represent a load mark, a pattern of rill marks, or some other inorganic sedimentary structure.

The specimen resembles the oral surface of a single lobe of *Inaria karli* Gehling, 1988 in size, preservation in negative hyporelief, and the plumose arrangement of longitudinal ridges, but differs in exhibiting a single rather than double border and in several other respects. Broad comparisons can also be made with *Lomosovis* Fedonkin, which, however, is parallel-sided rather than petaloid and also differs in the pattern of ridge development. The range of morphology of the Plumose Problematicum is unknown, as it is presently known only from a single, fragmentary specimen.

The Plumose Problematicum probably represents a bag-shaped organism that was folded longitudinally during burial.

ICHNOFOSSILS

Ichnogenus *AULICHNITES* Fenton and Fenton, 1937

Type ichnospecies. *Aulichnites parkerensis* Fenton and Fenton, 1937.

Aulichnites ichnosp.

Plate 3, figs 1 and 3

Description. Ten specimens preserved in positive relief. Unbranched, horizontal, sinuous to irregularly meandering, 10–11 mm wide bilobate trails; one specimen passing laterally into a trilobate trail. Smooth lobes separated by a median furrow 2–3 mm wide. Cross-sectional shape indeterminate, despite sectioning.

Remarks. Specimens are approximately twice as large as those figured by Fedonkin (1980, pl. 1, figs 3–5; 1985c, pl. 26, figs 1 and 8) from the Vendian of the White Sea area, but are otherwise similar. They are similar to the type species, *A. parkerensis*, in size and overall morphology, but differ in the absence of curved striae on the surface of the lobes. Some of the type specimens of *A. parkerensis*

EXPLANATION OF PLATE 3

- Figs 1 and 3. *Aulichnites* sp., epirelief. Locality 13, Sekwi Brook North. 1, GSC 95913, $\times 1$. 3, GSC 95914, $\times 1$.
 Fig. 2. *Helminthopsis abeli* Książkiewicz, 1977, hyporelief. Locality 26, Sekwi Brook South, GSC 95915, $\times 0.75$.
 Fig. 4. *Eoporpita* sp., hyporelief. Locality 3, Sekwi Brook North, GSC 95916 (lower left), GSC 95917 (upper right), $\times 1$.
 Fig. 5. *Planolites montanus* Richter, hyporelief. Locality 30, Majesty Section, GSC 95918, $\times 1$.
 Figs 6–8. *Palaeophycus tubularis* Hall. 6, hyporelief, locality 13, Sekwi Brook North, GSC 95919, $\times 1$. 7, hyporelief, locality 30, Majesty Section, GSC 95920, $\times 1$. 8, cross-section of 7 showing thin clay lining and partial collapse.
 Fig. 9. *Neonereites*? sp. and *Planolites montanus*, hyporelief. Locality 11, Sekwi Brook North, GSC 95921 and 95922, $\times 1.5$.



1



2



3



4



5



6



7



8



9

exhibit a unilobed lower surface (Hakes 1977), a feature not determinable on the present material. These preservational features preclude identification of the Sekwi Brook specimens to the ichnospecies level.

Aulichnites is generally interpreted as the grazing trail of a gastropod (Fenton and Fenton 1937; Häntzschel 1975; Howard and Frey 1984) or similar organism. Yochelson and Schindel (1978) doubted this interpretation, but did not offer specific reasons for their view. *Aulichnites* also ranges throughout the Phanerozoic (Häntzschel 1975). It occurs most commonly in shallow marine deposits (Hakes 1977), but is also found in deep-water turbidites (Hill 1981).

Ichnogenus HELMINTHOIDA Schafhäütl, 1851

Type ichnospecies. *Helminthoida labyrinthica* Heer, 1865.

Helminthoida ichnosp.

Plate 4, fig. 1

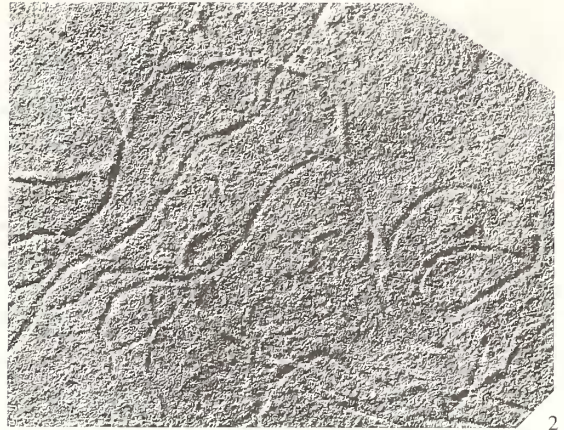
Description. One specimen preserved in part and counterpart, and a second uncollectable specimen studied in the field. Unbranched, unlined, horizontal meandering burrows 2.1–2.9 mm wide, with smooth surface and fill similar to host lithology. Meanders increasing in amplitude distally from 100–150 mm; wavelength 40–60 mm. Adjacent burrow segments parallel to sub-parallel.

Remarks. *Helminthoida* is a regularly meandering, hemicylindrical trace that shows a strong tendency towards development of parallel meanders (Häntzschel 1975; Książkiewicz 1977). As such, it can readily be distinguished from *Taphrhelminthoida* Książkiewicz (which is bilobate) and *Helminthopsis* Heer (which is less regularly meandering). The specimens of *Helminthoida* from Sekwi Brook display the meandering habit diagnostic of the ichnogenus, but are considerably larger and exhibit more open meanders than most Phanerozoic specimens (but see the Early Cambrian specimens of *H. miocenica* in Crimes and Anderson 1985, figs 7.3–7.5). Seilacher (1974, 1977) has documented similar trends in the evolution of other meandering trace fossils such as *Nereites*, and has related it to a gradual decline in body size and increase in behavioural complexity in deep-sea environments throughout the Phanerozoic.

Helminthoida is a characteristic element of Cretaceous-Tertiary flysch deposits (e.g. Seilacher, 1964; Książkiewicz 1970, 1977; Crimes 1977) and also occurs in Recent deep-sea sediments (Chamberlain 1975). It has been reported from Ordovician and Silurian flysch (Pickerill 1980, 1981) and from Early Cambrian storm deposits of eastern Newfoundland (Crimes and Anderson 1985). Glaessner (1969) figured complexly meandering burrows from Ediacara under the name 'Form C'; these have been compared with *Helminthoida* by Crimes (1987) and are also quite similar to *Yelovichnus gracilis* Fedonkin, 1985c from the Vendian of the White Sea area. Fedonkin (1985c) has also figured specimens of *Helminthoida* ichnosp. from the same strata.

EXPLANATION OF PLATE 4

- Fig. 1. *Helminthoida* sp., hyporelief. Locality 10, Sekwi Brook North, GSC 95923, $\times 0.5$.
 Figs 2 and 3. *Helminthoidichnites tenuis* Fitch, epirelief. 2, locality 6, Sekwi Brook North, GSC 95924, $\times 0.5$.
 3, locality 19, Sekwi Brook South, GSC 95925, $\times 0.5$.
 Fig. 4. *Helminthopsis?* sp., epirelief. Locality 11, Sekwi Brook North, GSC 95926, $\times 0.5$.
 Figs 5 and 6. *Helminthopsis irregularis* (Schafhäütl), hyporelief. Locality 26, Sekwi Brook South. 5, GSC 95927, 1. 6, GSC 95928, $\times 0.75$.



Ichnogenus *HELMINTHOIDICHNITES* Fitch, 1850

Type ichnospecies. Helminthoidichnites tenuis Fitch, 1850

Helminthoidichnites tenuis

Plate 4, figs 2 and 3

- 1969 'Form B' Glaessner, p. 381, fig. 5B.
 ?1969 'Form E' Glaessner, p. 382, fig. 5F.
 1976 'crawling trails' Palij, pl. 26, figs 1 and 2.
 1979 'crawling trails, first variety' Palij *et al.*, p. 77, pl. 53, figs 2 and 4.
 1981 *Gordia* sp. Hofmann, p. 307, fig. 5B.
 1981 *Gordia?* sp. Hofmann, p. 307, fig. 5D.
 1983 *Gordia* sp. Fritz *et al.*, pl. 44.1, fig. 3.
 1985 *Gordia* sp. Crimes and Anderson, p. 321, fig. 5.8.
 1985c *Gordia* sp. Fedonkin, pl. 23, fig. 1.
 1987 *Gordia marina* Narbonne and Hofmann, pp. 668-670, text-fig. 10a
 1989a *Planolites* sp. Aitken, fig. 6C.
 1989 *Planolites beverleyensis* Gibson, p. 5, figs 3.8 and 4.1.

Description. Numerous specimens (47 measured) preserved in both positive and negative relief on the tops and soles of beds. Irregularly sinuous to meandering, smooth, unlined, cylindrical burrows 1.1-3.3 mm (mean = 2.1 mm) in diameter; diameter constant within a single specimen. Burrows commonly crossing adjacent specimens, and rarely (three examples) crossing previously constructed portions of the same specimen. Specimens preserved in negative epirelief with narrow levées. Specimens preserved in positive relief with fill similar to host lithology, and flanked by narrow grooves. True branching absent, but offset of crossing specimens commonly producing pseudobranches.

Remarks. *Helminthoidichnites* is herein used in the sense of Hofmann and Patel (1989) for irregularly sinuous to meandering burrows with random crossings of the same and adjacent burrows. As such, it differs from *Gordia* Emmons, 1844 which exhibits long parallel limbs with numerous over-crossings, and from *Helminthopsis* Heer, 1877 which is irregularly meandering but avoids level crossings of the same or adjacent burrows. The Sekwi Brook specimens are most similar to material from Ediacara described by Glaessner (1969) as 'Form B', and to *Gordia* sp. from the late Precambrian of the Burin Peninsula, Newfoundland (Crimes and Anderson 1985). Specific points of similarity include the size, presence of narrow levées, development of pseudobranches, and the tendency of burrows commonly to cross adjacent burrows but only rarely to cross themselves.

Helminthoidichnites is common in the Ediacaran, where it previously has been referred to *Gordia* or *Planolites* (see synonymy), and also ranges throughout the Phanerozoic (Hofmann and Patel 1989). It is eurybathic, and probably represents the crawling or feeding trail of a vermiform organism.

Ichnogenus *HELMINTHOPSIS* Heer, 1877

Type ichnospecies. Helminthopsis magna Heer, 1877 (but see Książkiewicz 1977, p. 116).

Helminthopsis abeli Książkiewicz, 1977

Plate 3, fig. 2

Description. Three specimens preserved in positive hyporelief. Smooth, unbranched, unlined, hemicylindrical burrows 6.0-6.3 mm in diameter, with burrow-fill similar to host lithology. Burrows loosely winding, with a tendency to meandering.

Remarks. The specimens closely conform in size and morphology to those illustrated by Książkiewicz (1977, pl. 12, fig. 5; text-fig. 21a-h). *H. abeli* ranges throughout the Phanerozoic, in rocks of both shallow-marine (e.g. Crimes and Anderson 1985) and especially deep-sea (e.g. Książkiewicz 1977) aspect. It had not previously been reported from the Precambrian.

Helminthopsis is an irregularly meandering burrow that avoids level-crossings (Książkiewicz 1977). The ichnogenus has been reported from the Precambrian of the Cassiar Mountains, northwestern Canada (Fritz and Crimes 1985) and the Carolina Slate Belt of the southeastern USA (Gibson 1989), and also ranges throughout the Phanerozoic (Häntzschel 1975). *Helminthopsis* is eurybathic, but is most commonly reported from deep-water flysch deposits (Pickerill 1981). It represents the feeding or grazing burrow of a vermiform organism, most likely an annelid (Książkiewicz 1977).

Helminthopsis irregularis (Schafhäütl), 1851

Plate 4, figs 5 and 6

Description: Numerous specimens preserved in positive hyporelief on eleven slabs. Burrows ranging from irregularly winding to tightly meandering with parallel arms and second-order windings, even within the same specimen. Burrows unbranched and unlined, with fill similar to host lithology, predominantly smooth but with local transverse markings. Burrow diameter 1.4–3.1 mm, with diameter constant within any single specimen. Cross-overs of the same or adjacent burrows absent.

Remarks. This ichnospecies was originally assigned to *Helminthoida* Schafhäütl. Książkiewicz (1977) regarded it as a very regular version of *Helminthopsis* rather than an irregular version of *Helminthoida*, a view with which we concur. *Helminthopsis irregularis* exhibits two behavioural approaches to avoid level-crossings (Pl. 4, figs 5 and 6). The most common approach is to cross at a stratigraphically higher or lower level than the previous burrow; this avoids crossings, but requires that the feeding organism leave the organic-rich bedding plane briefly. A less common, but more efficient method is the local development of subparallel meanders to avoid crossing over its own or an adjacent burrow. This represents a primitive version of *phobotaxis* (sensu Richter 1928), which characterizes meandering burrows in Phanerozoic deep-sea deposits (Seilacher 1967, 1974; Raup and Seilacher 1968).

H. irregularis has previously been described only from Mesozoic and Tertiary, deep-water flysch deposits (Książkiewicz 1977). Paczeńska (1988) listed, but has not yet figured or described, a possible specimen from the upper Proterozoic Lublin Formation of Poland.

Helminthopsis? ichnosp.

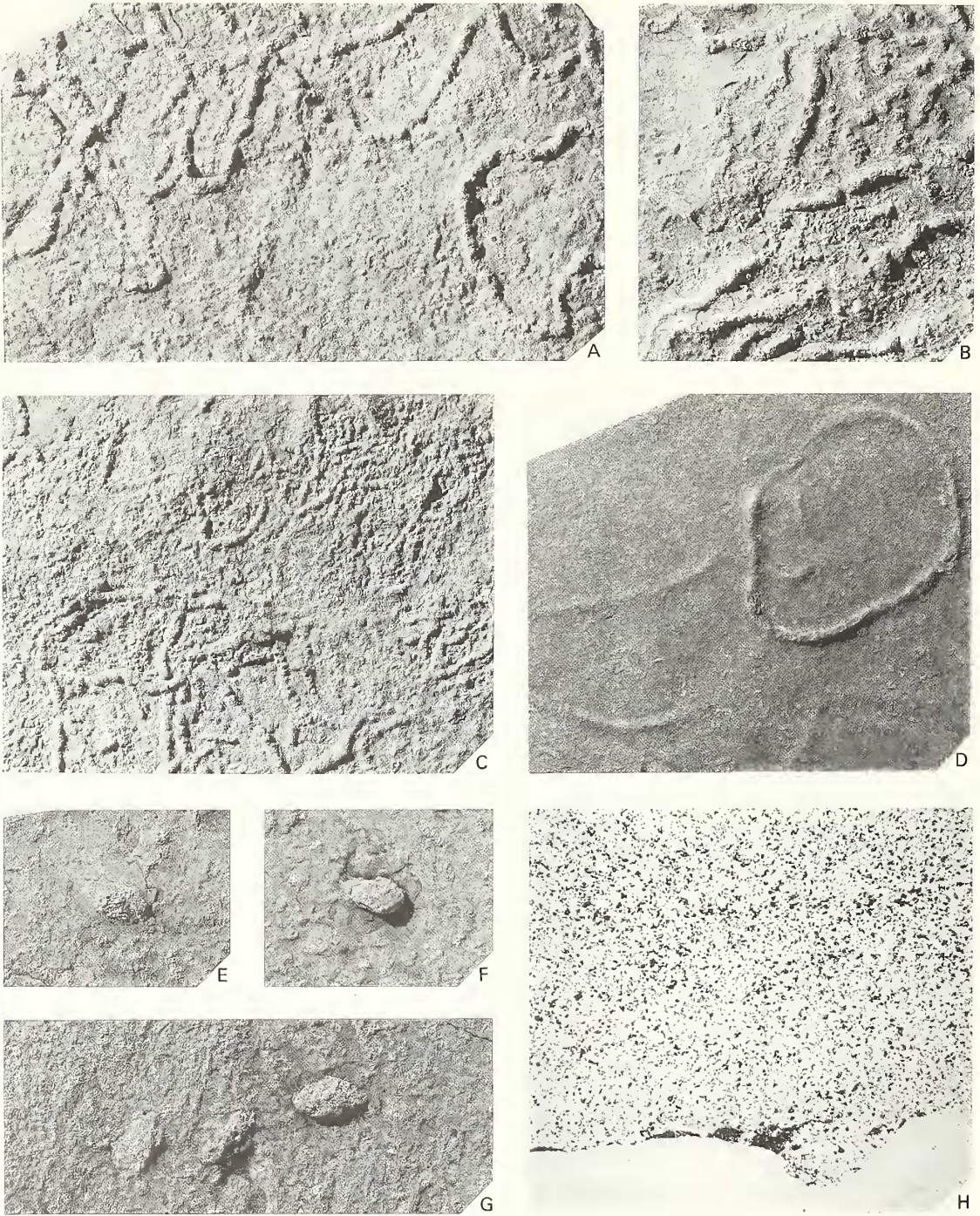
Plate 4, fig. 4

Description. One specimen preserved in negative epirelief. Horizontal burrow 2 mm in diameter consisting of a series of connected arcuate loops. Burrow flanked by narrow levées.

Remarks. The single specimen is most similar to one illustrated by Gibson (1989) from the deep-water Carolina Slate Belt of the southeastern U.S.A. Broad comparisons can also be made with *Gordia arcuata* Książkiewicz, 1977, but *Helminthopsis* sp. is considerably less arcuate with turnings confined to the horizontal plane.

Ichnogenus LOCKEIA James, 1879

Type ichnospecies. *Lockeia siliquaria* James, 1879.



TEXT-FIG. 7. A-C, *Torrowangea rosei* Webby, hyporelief; A, locality 29, Majesty Section, GSC 95929, $\times 1$; B, locality 15, Sekwi Brook North, GSC 95930, $\times 1$; C, locality 29, Majesty Section, GSC 95931, $\times 1$. D, Knotted circular burrow, hyporelief. Locality 11, Sekwi Brook North, GSC 95932, $\times 0.5$. E-H, *Lockeia* ichnosp., locality 13, Sekwi Brook North; E-G, hyporelief, GSC 95933-95937, $\times 2$; H, photomicrograph cross-section, GSC 95938, $\times 5$.

Lockeia ichnosp.

Text-fig. 7E-H

Description. Eight specimens preserved in positive hyporelief. Oblong bodies 4.3–5.6 mm (mean = 5.2 mm) long and 2.4–2.9 mm (mean = 2.7 mm) wide, with a constant length/width ratio of approximately 2:1. Specimens smooth and almond-shaped, with one rounded and one pointed end. Maximum relief 2.2 mm; burrow-fill structureless, and similar in composition to the overlying quartzarenite bed. Sandstone sole sharply upturned in the immediate vicinity of the burrow.

Remarks. This ichnogenus is referred to under the name *Pelecypodichnus* Seilacher by many workers, but we agree with Osgood (1970), Häntzschel (1975) and Maples and West (1989) that *Lockeia* is a valid name and the subjective senior synonym of *Pelecypodichnus*. The specimens from Sekwi Brook are similar to *L. amygdaloides* (Seilacher) in exhibiting an almond-shaped cross-section and a consistent 2:1 length/width ratio, but lack the keel present on some specimens of *L. amygdaloides*.

Based on its symmetry and comparisons with the burrows of modern bivalves, Seilacher (1953) concluded that *Lockeia* ('*Pelecypodichnus*') represents the resting burrow of a bivalve. Seilacher's view has been supported by virtually all subsequent workers (e.g. Osgood 1970; Eager 1974; Hakes 1976, 1977; Bromley and Asgaard 1979; Thoms and Berg 1985; Wright and Benton 1987), many of whom suggested specific bivalve genera as the originators of the *Lockeia* in their sections. The Sekwi Brook specimens of *Lockeia* exhibit typical bivalve symmetry, with a single plane of mirror symmetry that passes longitudinally through the structure. Another feature consistent with a bivalve origin is the upturning of the sole of the bed in the immediate vicinity of the burrow, and the associated upward pinch of clay drapes around the burrow (Text-fig. 7H). This feature has been described from Phanerozoic specimens of *Lockeia amygdaloides* (e.g. Bromley and Asgaard 1979, fig. 5B), and implies that the mode of burrowing was bivalve-like, and consisted of probing and penetration rather than excavation (Pojeta 1987).

Bivalves are the only extant organisms that exhibit both a cross-sectional shape and a mode of burrowing consistent with the Sekwi Brook specimens of *Lockeia*. However, the oldest confirmed bivalve body fossils are Early Cambrian (Pojeta *et al.* 1973; Pojeta 1985; Runnegar 1985). The presence of *Lockeia* in the Ediacaran implies either that very thin-shelled/poorly calcified bivalves evolved in the Late Precambrian, or that *Lockeia* could also be constructed by a now extinct group of organisms similar to bivalves in some morphological and behavioural aspects.

Lockeia is a facies-crossing ichnogenus that is known from a wide range of non-marine (e.g. Bromley and Asgaard 1979) and shallow to deep marine (e.g. Crimes 1977, table 4) settings.

Ichnogenus NEONEREITES Seilacher, 1960

Type ichnospecies. *Neonereites biserialis* Seilacher, 1960.

Neonereites? ichnosp.

Plate 3, fig. 9

Description. Two specimens preserved in positive hyporelief. Each specimen comprising a gently curved, uniserial string of hemispheres, 0.4–0.7 mm in relief and composed of fine sandstone similar to host lithology; adjacent hemispheres in contact. Hemispheres progressively increasing in size distally. Larger specimen 16.0 mm long, consisting of 7 hemispheres 1.2–3.5 mm in diameter; smaller specimen 8.1 mm long, consisting of 4 hemispheres 1.7–2.7 mm in diameter.

Remarks. The specimens are most similar to *Neonereites uniserialis* Seilacher, but differ in that hemispheres progressively increase in size along the chain. No similar forms of *Neonereites* have previously been described.

Neonereites is commonly reported from Ediacaran strata (Text-fig. 6), and also ranges throughout the Phanerozoic (Häntzschel 1975). It is a facies-crossing form (Seilacher 1964; Crimes 1977) which represents the feeding burrow of a vagile vermiform organism, probably an annelid (Hakes 1976).

Ichnogenus PALAEOPHYCUS Hall, 1847

Type ichnospecies. Palaeophycus tubularis Hall, 1847.

Palaeophycus tubularis Hall, 1847

Plate 3, figs 6–8

Description. Thirty-four specimens preserved in convex hyporelief and full relief. Straight, curved, to gently sinuous, horizontal, predominantly unbranched, hemicylindrical to cylindrical burrows, 3.7–7.1 mm (mean = 5.8 mm) in diameter. Preserved length up to 140 mm. Burrows smooth-walled and very thinly lined with clay, locally partially collapsed, and with fill similar to host lithology.

Remarks. The taxonomy of *Palaeophycus* has been reviewed by Pemberton and Frey (1982), who distinguished it from the similar ichnogenus *Planolites* Nicholson by the presence of a burrow-lining fill similar to the host lithology, and local evidence of partial burrow collapse. These features reflect passive filling of originally open burrow systems constructed by suspension-feeding or predaceous organisms, predominantly annelids (Pemberton and Frey 1982). *Palaeophycus* is common in Phanerozoic strata, where it occurs in virtually all sedimentary facies (Pemberton and Frey 1982). It is commonly reported in compilations as ranging in age from 'Precambrian to Recent' (e.g. Häntzschel 1975), but the only primary report of Precambrian *Palaeophycus* known to us is from the Risky Formation of the Wernecke Mountains (Nowlan *et al.*, 1985). The second variety of 'crawling traces' described by Palij *et al.* (1979, pp. 77–78, pl. 53, fig. 5; pl. 54, fig. 1) from the Vendian of Podolia is broadly similar, but further details of the nature of the burrow fill and the presence or absence of a burrow lining are necessary to determine whether it represents *Palaeophycus* or *Planolites*.

Ichnogenus PLANOLITES Nicholson, 1873

Type ichnospecies. Planolites vulgaris Nicholson and Hinde, 1875.

Planolites montanus Richter, 1937

Plate 3, figs 5 and 9

- 1970 'hypichnial and exichnial casts' Banks, p. 26, pl. 1*b,d*.
- 1970 'trails' Webby, pp. 87–88, fig. 3B–D, ?fig. 4*a–b*.
- 1972*a* 'threadlike trails' Germs, p. 208, pl. 26, figs 5 and 7, pl. 27, fig. 1.
- 1972*b* 'threadlike trails' Germs, p. 866, pl. 1, figs 5 and 7, pl. 2, fig. 1.
- 1973 'hypichnial and endichnial burrows' Banks, p. 4, fig. 4*a*.
- 1977 *Planolites* sp. Fedonkin, p. 184, pl. 2*d*.
- 1979 'crawling traces, third variety' Palij *et al.*, pp. 77–78, pl. 54, fig. 2.
- 1979 *Planolites* cf. *serpens* Palij *et al.*, p. 73, pl. 42, fig. 6.
- 1984 *Planolites* sp. Glaessner, p. 70, fig. 2/7.
- 1985*c* *Planolites* cf. *serpens* Fedonkin, pl. 28, figs 3 and 6.
- 1987 *Planolites montanus* Narbonne and Hofmann, pp. 670–671, text-fig. 10*b,d*.
- 1989 *Planolites montanus* Gibson, p. 5, fig. 4.1.

Description. Numerous specimens preserved in convex hyporelief and full relief. Burrows cylindrical, unbranched and unlined, and with structureless fill dissimilar to host lithology. Burrows highly sinuous and undulatory, occurring on bedding surfaces as small knobs and as discontinuous burrow segments typically less than 5 mm long (but ranging up to 55 mm long). Burrow diameter 0.3–1.7 mm (mean = 0.8 mm; $n = 120$).

Remarks. The taxonomy of *Planolites* was reviewed by Pemberton and Frey (1982), who recognized only three valid ichnospecies from among the thirty-three formally defined forms; several new ichnospecies have been named subsequently. The Mackenzie Mountain specimens fall within the diagnosis of *P. montanus* as 'relatively small, curved to contorted burrows' (Pemberton and Frey 1982, p. 870). *Planolites* is a eurybathic ichnogenus that could be produced by a wide variety of vermiform organisms (Alpert 1975; Pemberton and Frey 1982).

Planolites ranges in age from Ediacaran to Recent (Häntzschel 1975). *P. montanus* occurs throughout the Phanerozoic (Pemberton and Frey 1982, pp. 869–870) and is perhaps the most widely distributed Ediacaran ichnospecies (see synonymy).

Ichnogenus TORROWANGEA Webby, 1970

Type ichnospecies. *Torrowangea rosei* Webby, 1970.

Torrowangea rosei Webby, 1970

Text-fig. 7A–C

- 1981 *Torrowangea* sp. Hofmann, p. 309, fig. 5C.
- 1985 *Torrowangea rosei* Paczeńska, pl. 1, figs 1, 2, 5.
- 1986 *Torrowangea rosei* Paczeńska, p. 35, pl. 1, figs 1 and 4
- 1987 *Torrowangea* sp. Narbonne *et al.*, fig. 6C.
- 1989a *Torrowangea* sp. Aitken, fig. 6B.

Description. Numerous specimens preserved in positive hyporelief and rarely in negative epirelief. Sinuous to irregularly meandering, horizontal burrows. Burrows unbranched and unlined; cross-overs of the same or adjacent individuals occurring commonly, in some instances forming figure-8 pattern. Burrows 0.8–2.7 mm (mean = 1.8 mm; $n = 160$), with irregularly-spaced transverse constrictions resulting in a marked 'pinch-and-swell' appearance. Burrow-fill slightly coarser and better sorted than host lithology.

Remarks. *Torrowangea* sp. was described from the Sekwi Brook South section by Hofmann (1981) on the basis of relatively few specimens. Our analysis of several hundred specimens confirms Hofmann's generic identification, and further suggests that the material can be referred to *T. rosei*. Irregularly meandering and crossing specimens similar to Webby's (1970, fig. 18C) holotype occur rarely (Text-fig. 7A, C), but most specimens are sinuous (Text-fig. 7B) and are best compared with two of the paratypes figured by Webby (1970, fig. 18A, B) and with the specimens illustrated by Hofmann (1981) and Paczeńska (1985, 1986).

The present specimens slightly extend the range of burrow diameters for *Torrowangea* in both directions, but the mean is well within the range of the type material. The marked 'pinch-and-swell' appearance of *Torrowangea* was interpreted by Webby (1970) as a backfill structure, but this is not consistent with the apparent absence of internal structure in longitudinal thin sections of the Mackenzie Mountain specimens. Most likely, it reflects peristalsis.

Torrowangea was originally described from the Lintiss Vale Formation of New South Wales, Australia (Webby 1970). The age of this unit is controversial, with some authors favouring a latest Precambrian (probably Kotlin-equivalent) age and others favouring an earliest Cambrian (probably Rovno-equivalent) age (see review in Webby 1984). Narbonne and Myrow (1988) and Walter *et al.* (in press) believed that the presence of *Phycodes*? and other complex burrows favoured the latter

view. *Torrowangea* has been described from undoubted Precambrian strata (e.g. Paczeńska 1985, 1986), and from subtrilobite Lower Cambrian deposits (e.g. Aceñolaza and Durand 1973). Pemberton and Frey (1982) tentatively referred ?*Planolites octichnus* Chamberlain, 1971 from the Carboniferous of Oklahoma to *Torrowangea*; our examination of Chamberlain's specimens indicated that the pattern of meandering is similar but that the irregular transverse constrictions diagnostic of *Torrowangea* are not present.

Torrowangea represents the feeding burrow of a worm-like organism, probably an annelid. It occurs in both shallow-water and deep-water deposits, and is most common in fine-grained, muddy sandstones. In the Sekwi Brook area, specimens also occur in ribbon-bedded lime mudstone.

Knotted Burrow

Text-fig. 7D

Description. Single specimen preserved in positive hyporelief. Unlined(?) hemicylindrical burrow 3.1 mm in diameter forming an irregular circle 59–79 mm in diameter, and forming a crude 'knot' at the point of overcrossing. Three arcuate burrows radiating outwards more than 100 mm. Burrow fill similar to host lithology.

Remarks. The overall structure is unlike any known to us. The central circle is somewhat larger and less regular than *Circulichnis montanus* Vyalov, 1971, but is otherwise similar. *Circulichnis* ranges throughout the Phanerozoic (Fillion and Pickerill 1984), and is also figured under the name *Gordia arcuata?* from the late Precambrian of the Carolina Slate Belt (Gibson 1989, fig. 3.1). It is eurybathic, but is most commonly reported from deep-water settings (Fillion and Pickerill 1984).

Similarity between the diameters of the circle and the branches, termination of all the branches at the circle, and the extreme scarcity of arcuate burrows of similar size elsewhere in the Blueflower Formation, implies that central circular burrow and the radiating arcuate burrows are related. The arcuate burrows may represent different activity by the same species or even organism, or (less likely) may represent branches that pass off the circular knotted burrow at a higher stratigraphic level and descend rapidly to the level of the bedding surface.

CONCLUSIONS

1. Ediacaran fossils occur sporadically throughout approximately one kilometre of deep-water strata, encompassing the upper Sheepbed Formation to the top of the Blueflower Formation, in the Sekwi Brook area of northwestern Canada. At least eleven body fossil species and twelve ichnospecies are present in this interval.

2. Ediacaran megafossils at Sekwi Brook comprise mainly sessile, benthic polypoid and frond-like organisms along with a single, presumably pelagic, chondrophorian. The occurrence of a predominantly *in situ* benthic fauna in muddy slope deposits below storm wave-base is not consistent with the hypothesis that these taxa functioned exclusively as photoautotrophs.

3. The Sekwi Brook megafossil assemblage is broadly similar to that reported from coeval shallow shelf deposits in the Wernecke Mountains, Flinders Ranges and Russian Platform, but apparently lacks the (?)actinian impression *Beltanelliformis* which is abundant in Ediacaran shallow shelf deposits. Similarity of Ediacaran assemblages in shelf and slope settings implies that the organisms had broad palaeoenvironmental ranges, and enhances their correlation potential.

4. The occurrence of a relatively diverse trace fossil assemblage at Sekwi Brook implies that the initial radiation of infaunal organisms extended into slope settings. The ichnocoenoses includes irregularly and regularly meandering burrows, and may represent a primitive version of the *Nereites* ichnofacies, which characterizes deep-water Phanerozoic deposits.

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